COMPARATIVE SPRING MIGRATION ARRIVAL DATES IN THE TWO MORPHS OF WHITE-THROATED SPARROW

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ABSTRACT.—White-throated Sparrows (*Zonotrichia albicollis*) display a plumage dimorphism (*white-striped* and *tan-striped*) with attendant behavioral differences, including greater aggression levels in white-striped birds and negative assortative mating, in which tan-striped birds pair with white-striped birds. To determine whether morph influences migration timing, which could influence patterns of assortative mating, we evaluated the phenology of northbound migration among White-throated Sparrows from a long-term banding dataset collected at a southern Ontario banding station. White-throated Sparrows are sexed by wing-chord length, but there is an intermediate size for which sex cannot be assigned. When all birds were considered together (both known and unknown sexes, $n = 6,243$), the white-striped birds migrated earlier by slightly more than 2 days. The sexing criteria, however, appeared to yield a sample that was not representative of the whole population: when we included only birds for which sex was assigned ($n = 2,794$, 45% of all birds), white-striped birds apparently migrated earlier by more than 4 days, but separate analyses of males ($n = 1,511$) and females ($n = 1,283$) revealed no differences in migration timing between morphs. By measuring wing-chord lengths of internally sexed specimens (from the Royal Ontario Museum) collected during April to June ($n = 273$), we found that in both sexes the wings of white-striped birds were about 2% longer than those of tan-striped birds. When we used these specimen data to recalibrate the sexing criteria, (a) it was possible to assign sex to 1.47 times as many birds ($n = 4,121$; 66% of all birds), (b) sex ratios of the banded birds more closely approached what appears to be the natural sex ratio (approximately 1:1), and (c) within-sex analyses indicated that white-striped females migrate earlier than tan-striped females by about 1.3 days, whereas there was no statistical difference between male morphs in migration timing. *Received 25 April 2005, accepted 2 February 2006.*

The White-throated Sparrow (*Zonotrichia albicollis*) displays a plumage dimorphism (Lowther 1961) produced by an inversion in the second chromosome (Thorneycroft 1966). The two morphs are usually referred to as *white-striped* and *tan-striped*. The former has a gray breast and a bright white median crown stripe and supercilium, while the latter has a brown breast and a dull or tan-colored crown stripe and supercilium (Lowther 1961, Falls and Kopachena 1994). White-striped males are slightly heavier than tan-striped males and white-striped females, which are heavier than tan-striped females (Tuttle 1993). Thorneycroft (1975) showed that the nestling sex ratio was not significantly different from 1:1, and both morphs are represented nearly equally in adult populations (Falls and Kopachena 1994).

Ecological and behavioral differences between white-striped and tan-striped morphs include aggression levels, preferred breeding habitat, and patterns of parental care (e.g., Knapton and Falls 1982, 1983; Knapton et al.

1984; Kopachena and Falls 1993; Tuttle 1993; Falls and Kopachena 1994). In particular, white-striped males are most aggressive and tan-striped females are least aggressive (Kopachena and Falls 1993). Tuttle (2003) found that, compared to tan-striped males, white-striped males exhibited higher rates of attempted polygyny and intrusion into neighboring territories, and lower rates of parental care and mate guarding. Negative assortative mating occurs such that >95% of pairs comprise one bird of each morph (Lowther 1961, Falls and Kopachena 1994, Houtman and Falls 1994). It has been proposed that females of both morphs prefer tan-striped males, and that the negative assortative mating is facilitated, at least in part, by the ability of white-striped females to out-compete tan-striped females for tan-striped males (Houtman and Falls 1994).

Notwithstanding the lack of evidence demonstrating ratios that depart from 1:1 for sex or for morph, Falls and Kopachena (1994) found unequal numbers of the two types of breeding pair assortments in Algonquin Park, Ontario, with nearly 70% composed of white-striped males and tan-striped females. However, in another Algonquin Park study, Knap-

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ton and Falls (1982) found the ecological distribution of tan-striped males to be much broader than that of white-striped males. In addition, there is a male floater population that includes an unknown proportion of both morphs (Falls and Kopachena 1994).

Typical of males in migrant passerines, male White-throated Sparrows migrate earlier than females (Jenkins and Cristol 2002). Considering the higher aggression levels in both the male and female white-striped morph, earlier arrival times of white-striped birds at their breeding grounds would not be surprising. If white-striped males arrive before tan-striped males, they would have first choice of territory. If white-striped females arrive before tan-striped females, they would have first choice of males, allowing them to pair with the preferred tan-striped males. Thus, whether due to differences in latitudes of wintering ranges, different departure dates, or different rates of migration, timing of northbound (herein referred to as "spring") migration could represent one factor influencing negative assortative mating in this species.

Knapton et al. (1984) considered morph and sex when comparing arrival times of White-throated Sparrows at breeding territories in Algonquin Park. Their two-year study revealed no significant timing differences between male morphs, but there was an apparent difference among females, whereby white-striped birds arrived before tan-striped birds. They were reluctant to conclude whether white-striped females were actually migrating earlier or were merely detected earlier due to either their greater levels of aggression and vocal behavior or their earlier association with males.

Here, we report results of two independent, but related, investigations. We began by considering the issue of morph-specific migration timing. To do this, we used banding data from a bird observatory in southern Ontario to analyze passage dates of White-throated Sparrows during spring migration. We speculated that the apparent earlier arrival of white-striped females on the breeding grounds reflects real differences in migration timing; thus, we predicted that white-striped females pass through earlier than their tan-striped counterparts. When our results suggested problems with the sexing criteria (wing-chord

length), we used museum specimens to investigate size differences between the two morphs to propose new morph-specific sexing criteria for the species. With these new rules, we reassigned sex to the birds in the banding data set and then repeated the analyses.

METHODS

Banding dataset.—We used White-throated Sparrow banding data collected at Long Point Bird Observatory (LPBO; 42° 35′ N, 80° 15′ W) on Lake Erie in southern Ontario. This species breeds north of LPBO, so passage times there were used as a proxy for arrival times at the nesting grounds. Observatory mist nets were opened on or near 1 April, prior to the mid-April arrival of the first White-throated Sparrows. Characteristics recorded at LPBO included wing-chord length, morph, weight, sex (by wing chord), date, and bander information.

Morph data were collected from 1981 through 1994, so we restricted our analysis to that period. We arbitrarily required a minimum of 25 individuals of each sex per spring migration to include that year's records in the dataset, which reduced the dataset to 6 years (1985–1986, 1991–1994). The White-throated Sparrow is dimorphic at least during spring migration and breeding (Atkinson and Ralph 1980, Falls and Kopachena 1994), which permitted morph assignment to 85% of the LPBO birds. Even though licensed banders train and supervise volunteers, non-assignment of morph probably was due to bander uncertainty in cases where birds with more intermediate plumage were caught. Furthermore, there may be instances in the datasets of incorrect morph assignment, although we think such mistakes would be unlikely during spring migration, when birds are in fresh plumage.

Following convention, the sexing technique used by banders at LPBO was based on wing-chord length (to the nearest mm) of the closed, unflattened wing chord, as measured from the most anterior point of the wrist joint to the tip of the longest primary. Birds of both morphs were sexed as male if the wing chord was ≥74 mm and as female if the wing chord was ≤68 mm. Birds with wing chords of 69–73 mm were designated as unsexed. We used chi-square analyses to determine whether the ratio of males to females in each morph differed

from a 1:1 ratio. Julian dates were used for passage dates, and we followed convention by setting alpha levels at 0.05 and reporting means as ± SE.

Analysis of migration timing.—We conducted four one-way analysis of variance (ANOVA) in three analyses to determine whether white-striped and tan-striped birds arrived at different times and, if so, whether sex was a factor. We used all birds in the first analysis, pooling both sexed and unsexed birds ($n = 6,243$). In the second analysis, we used only sexed birds, but we pooled both sexes ($n = 2,794$). In the third analysis, we did not pool sexes so that we could examine migration phenology for males ($n = 1,511$) and for females ($n = 1,283$) separately.

Re-calibrating the sexing criteria.—Initial analyses (see below) indicated that using the established sexing criteria would not allow an impartial test of differences in migration timing between the two morphs. We surmised that there were slight size differences between the morphs that might be confounding the analyses. If true, using the established sexing criteria would result in samples that were not representative of the population. Because females are smaller than males, it seemed likely that if tan-striped birds were smaller than white-striped birds, the sexing criteria would bias designations of tan birds as female and white birds as male. Accordingly, we investigated the possibility of devising a more accurate, morph-specific sexing system by re-calibrating the sexing criteria and then repeating the second and third analyses.

We obtained White-throated Sparrow skins ($n = 273$) from the Royal Ontario Museum (ROM) in Toronto, Ontario, Canada, to calibrate wing-chord length with sex and morph. Only birds collected during spring (April to June of each year) were used, and all specimens had been assigned sex based on examination of gonads rather than by wing chord. The length of the unflattened wing chord was measured three times for each bird, resulting in a mean measurement (to the nearest mm) that we used in our analysis. We used ANOVA to determine whether there was a within-sex difference in wing-chord length between white-striped and tan-striped birds.

We plotted wing-chord lengths of males and females, by morph, in a histogram to examine the range in overlap. We assumed a normal distribution within each sex of the ROM specimens. By convention, we accepted a two-tailed alpha level of 0.05, which allowed error rates of 2.5% on the upper end of the females' distribution and on the lower end of the males' distribution. These measurements were used to set new morph-specific measurements of wing-chord length for sexing the birds.

To determine whether the morph-specific sexing criteria yielded fewer unsexed birds, we used a one-sample sign test to compare the tallies of male, female, and unsexed birds assigned via the new criteria to those assigned via the established criteria. Specifically, we wished to see whether the new criteria increased numbers of white-striped females and tan-striped males. Chi-square analysis was used to determine whether the ratio of males to females in each morph differed from 1:1 after the proposed sexing criteria had been applied to the LPBO dataset. Once we determined that the morph-specific sexing criteria were superior, as demonstrated by substantial increases in sample sizes, we applied them to the LPBO data. Because we expected migration passage to be normally distributed (Mills 2005), we expected the distribution of accumulated percentages of migrants to be sigmoid; thus, we applied a third-order polynomial model to our distributions. Once such curves were estimated from the data, we compared morph passage times by comparing respective areas under morph-specific curves by using integrals.

RESULTS

Migration phenology using the established sexing criteria.—White-striped birds slightly outnumbered tan-striped birds in the banding dataset (56% white-striped). Using all banded birds for which morph was assigned ($n = 6,243$), there was a significant difference in the arrival times of the two morphs ($F_{1,6241} = 119.7$, $P < 0.001$). White-striped birds arrived 2.15 days earlier than the tan-striped birds (white-striped CI: 0.25 days; tan-striped CI: 0.30 days).

Using the established sexing criteria, only about 45% of the birds were sexed, and there were significantly fewer white-striped birds sexed as females than as males ($n = 1,561$, 29% female; $\chi^2 = 279.9$, df = 1, $P < 0.001$)

TABLE 1. Number of male, female, and unsexed White-throated Sparrows of both tan-striped and white-striped color morphs, identified according to established and re-calibrated sexing criteria. Birds were captured and banded at the Long Point Bird Observatory (LPBO), Long Point, Ontario (6 years: 1985–1986, 1991–1994).

| | White-striped birds | | | | Tan-striped birds | | | |
| | Established | | Proposed | | Established | | Proposed | |
Sex	n	Percent	n	Percent	n	Percent	n	Percent
Female	450	13.0	760	21.9	833	30.0	833	30.0
Male	1,111	32.0	1,560	45.0	400	14.4	968	34.9
Unsexed	1,909	55.0	1,150	33.1	1,540	55.5	972	35.1
Total	3,470				2,773			

and significantly more tan-striped birds sexed as females than as males (n = 1,233, 68% female; χ^2 = 152.1, df = 1, P < 0.001). Furthermore, the apparent migration timing differences between morphs were exaggerated when only sexed birds were pooled and analyzed, with white-striped birds apparently migrating 4.27 days earlier than the tan-striped birds ($F_{1,2792}$ = 192.7, P < 0.001). Finally, when separate analyses were conducted for males and females, apparent differences in migration timing between morphs were <1 day in both cases, and neither was statistically significant (males: $F_{1,1509}$ = 2.71, P = 0.10; females: $F_{1,1281}$ = 3.19, P = 0.074). Accordingly, we concluded that the sexed samples were neither reliable nor representative of the population, and we resorted to museum skins to see whether more reliable sexing criteria could be employed.

Re-calibrating the sexing criteria.—Analysis of the ROM skins showed that the wing chords of white-striped females (n = 46; 68.93 mm ± 0.63) significantly exceeded those of tan-striped females (n = 55; 67.61 mm ± 0.65) by an average of 1.32 mm ($F_{1,99}$ = 8.30, P = 0.005). The difference in male wing-chord lengths was also significant ($F_{1,170}$ = 25.8, P < 0.001), with those of white-striped birds (n = 99; 73.31 mm ± 0.43) averaging 1.48 mm longer than those of tan-striped birds (n = 73; 71.84 mm ± 0.34). In both sexes, the average wing-chord length of white-striped morphs was ~2% greater. Using the new sexing criteria and accepting a 2.5% error rate, we determined that we could not assign sex to white-striped birds with wing-chord lengths of 70–72 mm, nor to those of tan-striped morphs with wing-chord lengths of 69–71 mm.

When we reapplied the revised sexing criteria to the LPBO data and conducted a one-sample sign test on the data, 1.47 times as many birds were sexed, a significant increase (white-striped: n = 3,470, df = 1, P < 0.001; tan-striped: n = 2,773, df = 1, P < 0.001). In addition, sex ratios were less skewed for both morphs: the percentage of females increased modestly among white-striped birds (29% to 33%) and decreased dramatically among tan-striped birds (68% to 46%; Table 1). In both morphs, however, sex ratios still differed from a 1:1 ratio (white-striped: n = 2,320, χ^2 = 275.9, df = 1, P < 0.001; tan-striped: n = 1,801, χ^2 = 10.1, df = 1, P = 0.001).

Using the new sexing criteria, we repeated the second ANOVA by pooling males and females for both white- (n = 2,320) and tan-striped (n = 1,801) morphs and comparing phenologies by morph. White-striped birds passed LPBO 2.06 days earlier than tan-striped birds ($F_{1,4119}$ = 67.7, P < 0.001). Accordingly, we concluded that the samples sexed by using the new sexing criteria were representative of the whole population, because 2.06 days (calculated using only sexed birds) is very close to 2.15 days (calculated using all birds) and substantially different from the 4.27-day difference in migration timing (calculated using only birds sexed with the established sexing criteria).

Migration phenology using the re-calibrated sexing criteria.—Being satisfied with the new sexing criteria, we repeated the third analysis by comparing the within-sex passage dates for both morphs. Progression of the spring passage for the four sex-morph classes of White-throated Sparrow at LPBO is shown in Figure 1. As expected, third-order polyno-
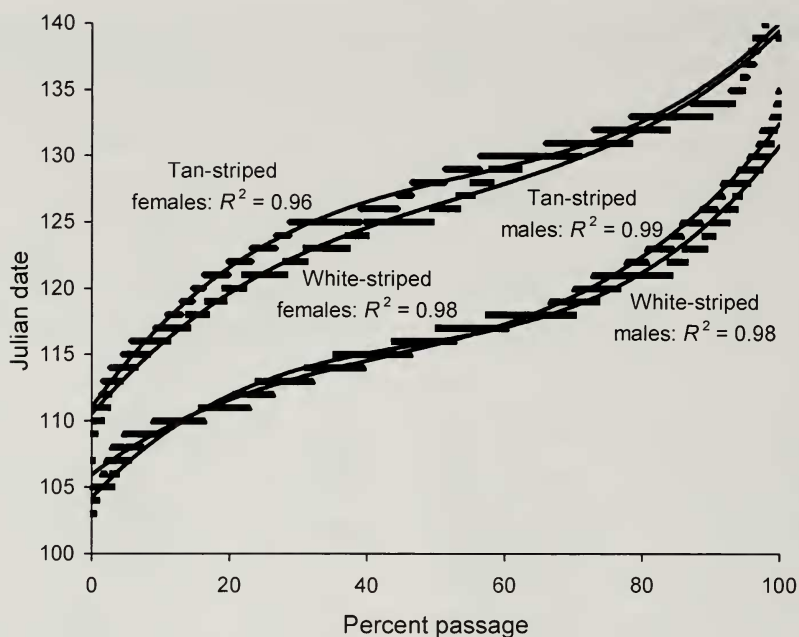
FIG. 1. Progression of spring (northbound) migration among sexes (females: the two upper curves; males: the two lower curves) and color morphs of White-throated Sparrows caught and banded at Long Point Bird Observatory, Long Point, Ontario. Birds were identified on the basis of sex and morph using re-calibrated sexing criteria (see text). The curves represent 3rd-order polynomials that describe the timing of each group's passage (R^2 values range from 0.96 to 0.99). For each curve, bar widths represent the proportion of birds passing through on each particular Julian date. Compared with tan-striped females, passage was significantly earlier for white-striped females ($n = 1,593$, $F_{1,1591} = 13.8$, $P < 0.001$) by about 1.3 days; there was no difference in arrival time of male morphs ($n = 2,528$, $F_{1,2526} = 2.25$, $P = 0.13$). Tan-striped females took 7% longer than white-striped females to complete their migration (see text).

mials described the migration timing well, with the four R^2 values ranging from 0.96 to 0.99. Using the 1st day of female migration as time zero and calculating the areas under each such curve by using integrals, tan-striped females took 7% longer than white-striped females to complete their migration. On average, this amounted to a significantly later arrival (1.3 days, $n = 1,593$, $F_{1,1591} = 13.8$, $P < 0.001$). Likewise, the passage of tan-striped males was 2.6% longer than that of white-striped males ($n = 2528$, $F_{1,2526} = 2.25$, $P = 0.13$).

DISCUSSION

Several studies of aggression levels among white-striped and tan-striped morphs in White-throated Sparrows revealed that both sexes of the white-striped morph appear to be more aggressive than their tan-striped counterparts (e.g., Watt et al. 1984, Kopachena and Falls 1993, Collins and Houtman 1999). To this body of knowledge we add the observation that white-striped females arrive at the breeding grounds earlier than tan-striped females. Our results are consistent—for both male and female arrival dates—with those of Knapton et al. (1984), who detected (a) white-striped males slightly, but not significantly, earlier than tan-striped males, and (b) white-striped females significantly earlier than tan-striped females. Results of our study, however, point to real differences in female migration timing, rather than differences in detections of white-striped and tan-striped birds.

Since male arrival dates are similar for both morphs, perhaps it is the earlier arrival of white-striped females that facilitates the negative assortative mating in this species. This is consistent with the mechanism proposed by Houtman and Falls (1994), whereby white-striped females out-compete tan-striped females for the tan-striped males. We suggest, however, that dominance does not act alone;

rather, the morph-specific migration phenologies also give a competitive advantage to white-striped females. While the 1- to 2-day difference in timing that we report here is modest, it is not implausible that it is sufficient to confer on white-striped females a competitive advantage over their tan-striped counterparts.

Early arrival can confer a higher social status in migrant birds (e.g., Red-winged Blackbirds, *Agelaius phoeniceus*; Cristol 1995). In White-throated Sparrows, Watt et al. (1984) concluded that the dominance between female morphs is seasonally dependent, whereby white-striped females are dominant on the breeding grounds and the tan-striped females are dominant on the winter grounds. The earlier spring arrival of white-striped females may then represent the switch in social status between female morphs. Inferior social status on the winter grounds could mean that the best strategy for white-striped females is to leave earlier in spring to attain a higher social status than tan-striped females. Others have concluded, however, that morph type has no effect on social rank in winter (Piper and Wiley 1989).

Alternatively, we acknowledge the possibility that the earlier arrival of white-striped females demonstrated in our study is merely facilitated by their larger size and may have no functional significance in negative assortative mating or dominance relationships. We think this unlikely, however, because white-striped males are bigger than tan-striped males, and yet their migration phenologies do not differ.

Because white-striped females exhibit lower levels of parental care than tan-striped females in normal, two-parent nests, Knapton and Falls (1983) questioned the ability of white-striped females to raise broods on their own without a mate. If true, fledging success among white-striped females might be enhanced if they pair with tan-striped males, as the latter exhibit parental contributions that match those of white-striped females and exceed those of white-striped males (Knapton and Falls 1983). In another study, however, Whillans and Falls (1990) found that both white-striped and tan-striped females compensate in terms of parental care when males are removed from the nest, and both female

morphs are able to successfully fledge young. Whillans and Falls (1990) suggested that the difference in results between the two studies might be explained by differences in study sites that supported differing densities of white-striped males.

Previously, researchers have suggested that nearly 70% of all White-throated Sparrow pairs are composed of white-striped males and tan-striped females (Thorneycroft 1975, Knapton and Falls 1983). This is perplexing, since the nestling ratio and the banding data we present suggest that the morph ratio is much closer to 1:1. It is not known whether tan-striped birds are predominant among populations of floating males, or whether white-striped birds are predominant among populations of non-breeding females. White-striped birds are more conspicuous compared to their tan-striped counterparts in song, territorial behavior, and overall brightness in color (Lowther 1961, Falls and Kopachena 1999), and this may influence apparent proportions of pair-assortment types.

With white-striped birds being larger and having significantly longer wing chords, we feel it would be logical to use two sexing systems when wing-chord length is employed. Rising and Shields (1980) found that, generally, tan-striped males were slightly smaller overall than white-striped males, and that generally white-striped females were larger than tan-striped females in terms of most characteristics that they measured. To assist in more comprehensive sex assignment and to generate samples more accurately representing natural populations, we suggest that these new sexing criteria be used whenever morph identification is possible. Although the sexing criteria proposed here yielded only slightly different wing-chord lengths than those measured by the established sexing criteria, implementing this change substantially increased the number of birds to which we could assign sex. When morph identification is not possible, the established wing-chord rule, as suggested in Pyle (1997), should be used.

Previously, it was known that there are several differences between white-striped and tan-striped morphs of White-throated Sparrows, including size, habitat, aggression levels, and parental care (Rising and Shields 1980, Knapton and Falls 1982, Houtman and

Falls 1994). Our study reveals yet another difference: the timing of spring migration among females differs between morphs. Overall, it appears that the White-throated Sparrow's morph-based systems of migration timing and social structure are unique among passerine birds.

ACKNOWLEDGMENTS

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